STUDIES OF THE GENUS *KATELYSIA* RÖMER 1857 (MOLLUSCA, LAMELLIBRANCHIATA).

By Barbara J. Nielsen.

Introduction.

There has been confusion as to the validity of the species included in the genus *Katelysia* Römer 1857, and this suggested the necessity for an assessment of its representatives in Victoria. This was followed by detailed studies of two particular species *Katelysia scalarina* Lamarck 1818 and *Katelysia rhytiphora* Lamy 1935 to ascertain their validity as biological or 'natural' species as against specific separation based on shell morphology alone. This includes the anatomy of the animals, statistical analyses of shell measurements and an investigation of breeding cycles. The third species *K. peronii* Lamarck 1818, is omitted because of insufficient material.

Synonymy.

Although Eduard Römer established the genus *Katelysia* for a group of *Venus* like lamellibranchs from southern Australia (genotype *K. scalarina* Lamarck 1818) in 1857 the name does not appear again in the literature until 1914 when Jukes-Brown used it in his revision of the family Veneridae. Later Lamy (1935, 1937) revised the Lamarkian species consigned to it. Unfortunately, Lamy's work was by-passed by Australian conchologists, most basing their check-lists on Pritchard's and Gatliff's condensation (1903) of nine Lamarckian species of Venus into three species, *Chione strigosa*, *C. scalarina* and *C. peronii*. *Katelysia* first came into general usage in 1938, when Cotton and Godfrey revived the name and recorded three species from South Australia.

Because of the numerous writers it is easiest to consider first the species listed in the four latest works of Kershaw (1955), Macpherson and Chapple (1951), Allan (1950) and Cotton and Godfrey (1938). As Kershaw's listing follows that of Cotton and Godfrey no distinction will be made between these two groupings.

Macpherson and Chapple used the grouping of Pritchard and Gatliff (1903), substituting Römer's generic name *Katelysia* for that of *Chione*. Allan in 1950 not only extended the scope of the genus to include two extra species and also included *K. enigma* Iredale 1936, which she suggested is similar to *K. strigosa* Lamarck of Victoria and *K. corrugata* Lamarck of South Australia.

The two extra species listed by Allan are *K. gallinula* Lamarck 1818 and *K. lagopus* Lamarck 1818. The former species has already been placed in the genus *Tawera* by Marwick in 1927. Both species are clearly closely related and differ considerably from members of the genus *Katelysia*.

Unfortunately Allan does not give any reason for her inclusion of these two species in *Katelysia* but as they both have features characteristic of the genus *Tawera* it is preferable to leave them in this genus.

Katelysia enigma Iredale 1936 was first described from one rather old and worn valve from Port Jackson, possibly of sub-recent origin. The type has been examined by the writer and is considered to belong to the same species as *K. strigosa* (Macpherson and Chapple 1951) (= *K. corrugata* (Cotton and Godfrey 1938)). The species does not seem to be living in great numbers in Port Jackson although sub-recent specimens are relatively common.

The specific name *K. corrugata* Lamarck 1818 used by Cotton and Godfrey (1938) is pre-occupied. It was first given to a *Circe* by *Chemnitz* (1784) and later to a *Tapes* by Gmelin (1791). Chemnitz is not accepted by the International Commission of Zoological Nomenclature (Schenk and McMasters 1950) but *Tapes corrugata* Gmelin is still valid. The latter is a Mediterranean species.

Sowerby 1855 illustrated a shell which he called *Venus strigosa* Lamarck and which Pritchard and Gatliff (1903) and later authors have considered to be a synonym of *corrugata* Lamarck and thus available to replace it.

Lamy pointed out that the species illustrated by Sowerby as *Venus strigosa* Lamarck is not the same as that described by Lamarck (1818). The Lamarckian species does not possess the radial striations shown in Sowerby's figure and these are not present on the type in the Paris Museum, which is similar to *Venus aphrodina* and *V. scalarina*. Sowerby comments after his description of *V. strigosa* that Lamarck does not mention these radial striations and suggests he did not notice them. However, as Sowerby's *V. strigosa* conforms with Lamarck's description of *V. corrugata* it is hardly likely that Lamarck did not notice this prominent feature when describing *V. strigosa*.

Thus the species described by Lamarck as *Venus corrugata* was left without a name. Lamy (1935) proposed the name *Katelysia rhytiphora* for this species and Macpherson (1958) used Lamy's *K. rhytiphora* for the first time in Australian literature.

Jukes–Brown (1914) included *Marcia* (*Katelysia*) *regularis* Deshayes and *Marcia* (*Katelysia*) *decussatus* Deshayes in the same genus as *K. scalarina et al.* However they appear to be closer to *Hemitapes* Römer. Römer gives *Venus conularis* as the type of the genus *Hemitapes* while Lamy (1937) includes this species in *Katelysia*. From Delessert's illustration (1841) it would appear that the type is an old discoloured shell and therefore its true position is uncertain. This immediately casts doubt on the validity of Römer's genus *Hemitapes* but this is beyond the scope of the present paper.

It is proposed therefore, to accept Lamy's species *K. rhytiphora* and the following two Lamarckian species, *K. scalarina* and *K. peronii* in the genus *Katelysia*. Fortunately there is no doubt about the position of *K. scalarina* Lamarck, specimens having been compared with the type at the Musee d'histoire Naturelle, Geneva by courtesy of Dr. E. Binder.

The type of *K. peronii* was not available at Geneva and is presumably in Paris since Lamy (1937) mentions five species which according to Lamarck's label were collected in Australia by Peron and Lesueur (1803). *K. peronii* has been confused with *K. rhytiphora* and was also given as a variety of *K. scalarina* by May (1921).

The remaining Lamarckian species which have been included in the genus can either be regarded as synonyms of the three above mentioned species or rejected from the genus.

The type of *Venus tristis* Lamarck 1818 is at Geneva. Photographs by Dr. Binder show that the specimen does not resemble *K.scalarina* as suggested by Binder (personal communication) nor does it possess the radial striations of *K. rhytiphora* and *K. peronii*. Also the hinge line does not resemble that of the three above-mentioned species, the central cardinal tooth on the left valve being deeply bifurcated. In *Katelysia* it is only slightly bifid.

The supposed type of *V. elegantina* Lamarck 1818 resembles *V. tristis* very closely and it is suggested that these two belong to the same species. Their exact generic position is uncertain. Römer places them both in *Hemitapes*.

Katelysia peronii Lamarck 1818.

PLATE II., FIGS. 1–3.

Venus peroni Lamarck 1818 (p. 606, No. 81); Handle 1842 (p. 126); Menke 1843 (p. 44, No. 255); Philippi 1849 (vol. 3, pl. 8, fig. 8, 9).

Venus aphrodinoides Lamarck 1818 (p. 606, No. 82); Reeve 1864 (pl. 17, sp. 73).

Venus flamiculata Lamarck 1818 (p. 605).

Chione peronii Deshayes 1853 (p. 146, No. 81); Pritchard and Gatliff 1903 (p. 127, p. 94, pl. 15, fig. 9–10).

Chione aphrodinoides Deshayes (p. 148, No. 85).

Tapes victoriae Tension Woods 1878 (p. 55).

Marcia (Katelysia) aphrodinoides Lamy 1937 (p. 76).

Katelysia peronii Cotton and Godfrey 1938 (p. 243, Fig. 271); Allan 1950 (p. 331, pl. 39, Fig. 2); Macpherson and Chapple 1951 (p. 152); Kershaw, 1955 (p. 288, No. 189); Macpherson 1958 (p. 54, pl. 50 Fig. 7).

Shell ovate, tumid, more rounded than the other two species; sculptured with flat, slightly irregular ridges, crossed by faint radial costae. Shell colour cream with faint to irregular black angular marking not very clear. Inside the shell is cream to yellow with purplish markings.

Katelysia scalarina (Lamarck, 1818).

PLATE I., FIGS. 1–3.

Venus scalarina Lamarck 1818 (p. 599, No. 54); Delessert 1841 (pl. 10, fig. 12, a, b, c,); Hanley 1842, 1856 (p. 123, p. 358, pl. 16, fig. 4); Menke 1843 (p. 44, No. 254); Sowerby 1849–1855 (p. 736, No. 96, pl. 162, fig. 215–220; Reeve 1864 (pl. 20, sp. 96).

Venus aphrodina Lamarck 1818 (p. 605, No. 82); Delessert 1841 (pl. 11, fig. 1, a, b, c); Reeve 1864 (pl. 17, sp. 76).

Venus strigosa Lamarck 1818 (p. 605, No. 79).

Venus humphreyi Donovan 1834 (p. 16, pl. 78, fig. 2).

Chione scalarina Deshayes 1853 (p. 148, No. 86); Tate and May 1901 (p. 427); Pritchard and Gatliff 1903 (p. 127, p. 94, pl. 15, Fig. 7, 8).

Chione aphrodina Deshayes 1853 (p. 147, No. 84).

Marcia (Katelysia) scalarina Jukes-Brown 1914 (p. 88); Lamy 1937 (p. 75).

Marcia scalarina Hedley 1917 (p. M.24, No. 248); May 1921–1923 (p. 24, No. 178, pl. 10, Fig. 15).

Katelysia scalarina Cotton and Godfrey 1938 (p. 242, 243, Fig. 270); Allan 1950 (p. 331, 326, Fig. 77, No. 6); Macpherson and Chapple 1951 (p. 152); Kershaw 1955 (p. 228, No. 188), Macpherson 1958 (p. 14, pl. 10, Fig. 15).

Shell:

Equivalve, inequilateral, anterior dorsal margin less than half the length of the posterior dorsal margin. The angle at the umbos made by the two dorsal margins averages 114 deg. The ventral margin is smooth, flatly convex; the posterior and anterior margins are rounded. The hinge line is typical of the family Veneridae. There are three cardinal teeth on each valve—$\frac{\text{L } 101010}{\text{R } 010101}$ and no lateral teeth. The central cardinal tooth of each valve is bifid and does not extend to the ventral edge of the hinge plate. The angle between the posterior cardinal and

the central cardinal, in both valves, is more acute than that between the anterior cardinal and the central cardinal. All teeth are straight. The ligament is external, typical of the family. The lunule is narrow, lanceolate, well defined and the same colour as the rest of the shell. The escutcheon is long and smooth and prominent. Shell sculpture consists of concentric ridges parallel to the ventral margin, turned over except at the posterior end where they are produced into thin straight lamellae. There are no radial costae. Internally the adductor muscle scars and the pallial line are not very conspicuous. The posterior retractor muscle scar is sometimes partially separate from that of the posterior adductor muscle and easily distinguished in the shell. The anterior adductor muscle scar is elongate dorso-ventrally. Colouration is fairly consistent. The outside is very pale cream with faint grey black angular markings covering most of the shell. The inside is white with faint purple markings about the hinge and on the posterior margin. Some specimens from Port Arthur, Tasmania, were a uniform deep purple inside. It is suggested that this colouration is due to environmental conditions since examples of all three species from this locality show the same colouration.

Estuarine specimens from Lakes Entrance, Victoria (N.M. F1633) and the Tamar Estuary, Northern Tasmania, are distinguished by a thicker shell with broader, rounder, concentric ridges with no thin lamellae at the posterior end and the cardinal teeth are more deeply bifid. The outside of the shell is usually cream, the inside varying from pure white in Victorian forms to a very deep purple in some Tasmania forms.

Another variation is found in specimens from American River, Kangaroo Island. The shell resembles the type in having very similar sculpture and colouration but differs in outline, the anterior-posterior direction being strongly produced so that the shell forms a narrow ellipse.

It is possible that this variant is a separate race of the species but the differences are not sufficient to warrant the erection of a sub-species. However, a variety from south Western Australia is considered by the writer to be sufficiently distinct to be placed in a sub-species.

Katelysia scalarina sub-species polita sp. n.

Plate I., Figs. 4–6.

Shell similar to *Katelysia scalarina* s.s. in general outline and hinge area. " Concentric ridges less well defined than in *scalarina* senso stricto and not turned over to form sharp lamellae. Most shells show inconformity in sculpture indicating periodic breaks in the growth rate. Surface highly polished ".

The Holotype is in the National Museum of Victoria, No. F23499 and six paratypes No. F23500.

This sub-species is restricted to south-western Australia having been taken at Emu Point, Albany; Blackwood River, Augusta; Jervis Inlet; Nornalup and Novabiti Inlet near Perth.

FIG.1-DISTRIBUTION OF K SCALARINA

Distribution.

The distribution of *K. Scalarina* is shown on the accompanying map (Fig. 1). Apart from the living population extending from southern New South Wales to south Western Australia and Tasmania there is an extensive sub-recent fauna in the Pleistocene marine deposits of south-eastern South Australia (Crocker and Cotton, 1946) and also in Western Australia particularly on Rottnest Island.

In the area south of Mount Gambier to the east of Kingston extending sixteen miles inland from the present coastline, Crocker and Cotton record only one species, *K. scalarina*. However, in a collection seen in the Geology School, Melbourne University (collected Mr. A. A. Baker) from a deposit five miles west of Lake St. Claire, all three species were present, *K. scalarina* and *K. rhytiphora* predominating. Specimens of *K. scalarina* were typical sandy beach forms similar to those found at present in South Australia and Victoria.

Ecology.

This species is usually found in quiet, sheltered sandy bays and occasionally in estuarine conditions. While it has been collected from many localities it was necessary for purposes of study to choose a locality close to Melbourne. A sheltered bay on the north side of Mornington Jetty was found to be the most suitable. Here a large population of *K. scalarina* live in fine to medium grained sand about two to four centimetres below the surface, between the tide marks. At high tide they are covered by 0·3 to 1 metre of water.

The bay is shallow and crossed by several sand banks with occasional patches of *Zostera*. At the southern end of the bay there are patches of shingle and rock associated with the breakwater and the jetty.

K. scalarina appears to be restricted to the area between the tides. They are not uniformly scattered throughout the area but live in groups of half a dozen or more. Occasionally, specimens of *K. rhytiphora* are found in these groups but most occur in deeper water beyond the *K. scalarina*.

The associated fauna is similar to that of most sandy beaches in Port Phillip. Apart from *K. scalarina*, the dominant bivalve, *Amphidesma angusta* is also common between the tides. *Nassarius pauperatus* is the dominant gastropod while *Zeacumantis cerithium* appears in great numbers at certain times, but at others not at all. Other species recorded are *Conuber conicum, Cominella lineolata, Philine angasi*, and *Bullaria botanica*.

A prominent member of this community is an unidentified sea anemone attached to the posterior portion of the *K. scalarina* when they are buried in the sand. This anemone has also been found in the same association at Rosebud. It occurs in great numbers and proved a convenient means of detecting *K. scalarina*. It has not been found attached to neighbouring rocks where another, larger anemone, *Oulactis muscosa*, is common. In Tasmania, at Ralph's Bay this small anemone has been found attached to *Aloidis flindersi*.

ANIMAL MORPHOLOGY.

Although most zoologists are familiar with the general structure of the lamellibranch animal a fairly detailed description is included here because the members of the family Veneridae have not been described in detail. Most detailed descriptions are of the more primitive or more unusual families such as the Nuculidae and Mytilidae.

Mantle:

The animal is covered by the mantle, the two edges of which are completely free along the anterior and ventral margins. Posteriorly they join and are produced to form two siphons. Apart from the portion of the mantle ventral to the pallial line, the greater part consists of thin clear tissue containing some blood vessels but no extensions of the gonads as in *Mytilus*.

The mantle is attached to the shell valves along the pallial line by bands of muscle extending from the mantle edge for about 6 mm. to the pallial line. These bands of muscle are fine, closely set together and bifurcate several times before reaching the mantle edge.

The mantle edge is divided into three lobes (Yonge, 1948), an inner muscular lobe, a middle lobe which is thinner and less muscular, and an outer lobe which is thin and closely applied to the inside of the shell. The inner lobe is produced posteriorly to form the siphons and just anterior to the siphons divides into numerous finger-like processes.

The siphons are short and separate for most of their length. Their colour is white. On the outside they are covered for about half their length by scattered spots of black pigment. Inside, both siphons are lined with an epithelium, pigmented with bright yellow and varying amounts of black and bright orange.

The aperture of the exhalent siphon is encircled by a single row of small tentacles, the actual aperture being formed by a thin membrane capable of expansion during the expulsion of waste material. There are two rows of tentacles about the inhalent aperture; an outer one of small tentacles and an inner one of large tentacles, the small and large tentacles alternating with each other.

The internal openings of the siphons are wider than the external. The opening of the exhalent siphon is separated from that of the inhalent by a band of connective tissue which prevents the waste material contaminating the incoming current of water. Anteriorly and dorsally this connective tissue extends over the surface of the posterior adductor muscle covering the visceral ganglia and also supporting the nerves from the ganglia to the siphons.

Anteriorly the two mantle edges join near the ventral border of the anterior adductor muscle. Here the mantle is continuous with the connective tissue covering the posterior surface of the muscle and carrying the two nerves from the cerebral ganglia into the mantle edge.

The pericardial gland lies posterior to the umbos at the anterior end of the pericardial cavity. It is a reddish brown organ (White, 1928).

Gill Lamellae or Ctenidia:

The general form of the ctenidia is typical of the Veneracea. The axis extends from the region of the pericardial gland to the septum between the two internal openings of the siphons. The inner demibranch is also attached to the visceral mass along the dorsal side from the posterior end of the gill axis to the mouth. In *K. scalarina* this border of the inner demibranch is about 0·75 the length of the gill axis, while in *K. rhytiphora* it is aproximately equal to the length of the gill axis. This inner demibranch is much larger than the outer which has about half its surface area.

The ascending lamella of the outer demibranch has a super-axial extension (Ridewood, 1903) which covers the pericardial cavity and the kidney, in some animals being attached to the pericardium along its dorsal margin. The demibranches are strongly plicate.

Labial Palps:

The labial palps surround the mouth, there being two pairs—one dorsal, one ventral. Members of each pair are joined together by a strand of tissue. The surface of each palp is crossed by transverse ciliated ridges.

Kidneys:

The kidneys or renal organs are a pair of conspicuous brown triangular organs lying at the posterior end of the pericardial cavity, each covering a pedal retractor muscle.

Adductor Muscles:

The anterior adductor muscle is slightly smaller than the posterior. Both are composed of bundles of muscle fibres passing from one valve to the other and loosely held together by fine connective tissue. The bundles are composed of fine non-striated and striated muscle cells from 2 to 3 mm. long.

The Foot and Visceral Mass.

The foot and visceral mass are held in the shell by two pairs of muscles, the anterior and posterior pedal retractor muscles. The anterior pedal retractor muscles pierce the dorsal part of the mantle just posterior to the anterior adductor muscle and are attached to the shell slightly anterior of the anterior cardinal tooth below the hinge plate. The posterior pedal retractor muscles lie dorsal to and very close to the posterior adductor muscles. Usually on the shell the muscle scar of the posterior pedal retractor is so close to that of the posterior adductor that it is difficult to distinguish the two. However in some the two scars are partially separated.

The foot is best described as a hatchet shaped muscular bag, the ventral portion of which is composed mainly of muscles and blood vessels while the dorsal portion contains the gonads, alimentary canal and digestive glands. These are enclosed by a muscular wall which is composed of two sets of fibres diagonally crossing each other. One coat of fibres, the inner, arises from the anterior pedal retractor muscle and passes posteriorly to the ventral margin of the foot. The outer coat of fibres arises from the posterior retractor muscle and passes to the anterior ventral margin of the foot.

Internal Anatomy and Histology.

Alimentary Canal and Associated Organs:

The mouth opens on the anterior side of the visceral mass near the dorsal margin. It is compressed dorso-ventrally and opens into a narrow oesophagus which is about 3·5 mm. long. This is also compressed dorso-ventrally. It is lined with tall ciliated columnar epithelial cells resting on a thick basement membrane. Below this is connective tissue and muscle.

The oesophagus leads into the stomach, an irregularly shaped organ, 5·5 mm. long and 3 mm. high. The mid gut leaves the posterior end of the stomach on the ventral side, at 90 deg. to the long axis of the stomach.

The anterior portion of the stomach is covered completely by the three lobes of the digestive gland. This is a large pale green racemose gland 7 mm. by 5 mm. This gland is connected to the stomach by three wide ducts, one leaving on the left side and two on the right. The ducts leaving the stomach are broad thin-walled tubes. As they enter the gland they branch into several lobes and after further branching, end blindly as the digestive diverticulae. There appears to be a small caecum at the posterior end of the stomach between the openings of the right and left ducts separated from the opening of the right duct by a ridge. The gastric shield is on the posterior dorsal wall of the stomach and extends over the left side. Its presence was revealed in sections only.

The stomach is lined with a ciliated epithelium composed of tall narrow columnar epithelial cells. These cells have a prominent large, oval nucleus with a large nucleolus, most of the chromatin being concentrated about the periphery of the nucleus. The cilia are long and at their base there is a prominent row of basal granules. (Fig. 2.)

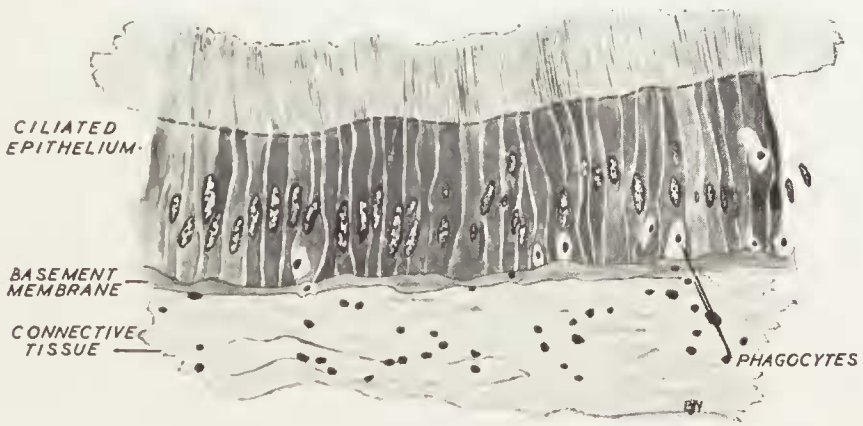

FIG. 2 - T.S. STOMACH WALL (*K. SCALARINA*) X 700

Beneath the gastric shield the cells are of the same histological type as the other epithelial cells although taller. It is doubtful whether cilia are present even though Yonge (1926) claims they are present in *Ostrea*.

In *K. scalarina* the cells beneath the shield, unlike those illustrated by Gutheil (1912, fig. 14, page 462) each have a prominent row of basal granules which are also seen in the adjacent cells not beneath the shield. Although Gutheil does not show the granules in his figure he mentions that there are various stages of degeneration in the epithelial cells. Yonge (1926) on the other hand shows both basal granules and cilia. According to Edmondson (1920) the cells beneath the gastric shield of *Mya arenaria* are not ciliated. Yonge (1926) found no mucus glands beneath the gastric shield although they were scattered through the rest of the stomach epithelium. As no mucus stains were used in this investigation the presence or absence of these cells has not been determined in *K. scalarina*.

The epithelium lining the larger ducts of the digestive gland is continuous with that of the stomach and is composed of similar cells. These cells are shorter and the cilia longer than those in the stomach. Phagocytes are numerous being scattered between the epithelial cells, in the basement membrane and the underlying circular muscles.

The ducts end in the digestive diverticulae which consist of bulbous blind tubules lined by large irregular non-ciliated cells which have a large, clear, round nucleus with a prominent large nucleolus. The cytoplasm of these cells is strongly vacuolated, often with food vacuoles. Phagocytes are common among these cells and also in the connective tissue surrounding the diverticulae. They are small with a darkly staining nucleus containing many granules of chromatin and surrounded by very little cytoplasm.

In cross-section the tubules are circular to ellipsoid, their lumen being also circular to ellipsoid, not tripartite or cruciform as described by Yonge (1926) in *Ostrea edulis*. The crypts of darkly staining cells mentioned by Yonge are not present. Instead, darkly staining cells occur about the periphery of the tubules, usually concentrated to one side or at either end. The remainder of the cells have a lightly staining cytoplasm. Yonge found in *Ostrea* that these dark staining cells were the younger cells, the areas in which they occur being areas of cell proliferation. (Fig. 3.)

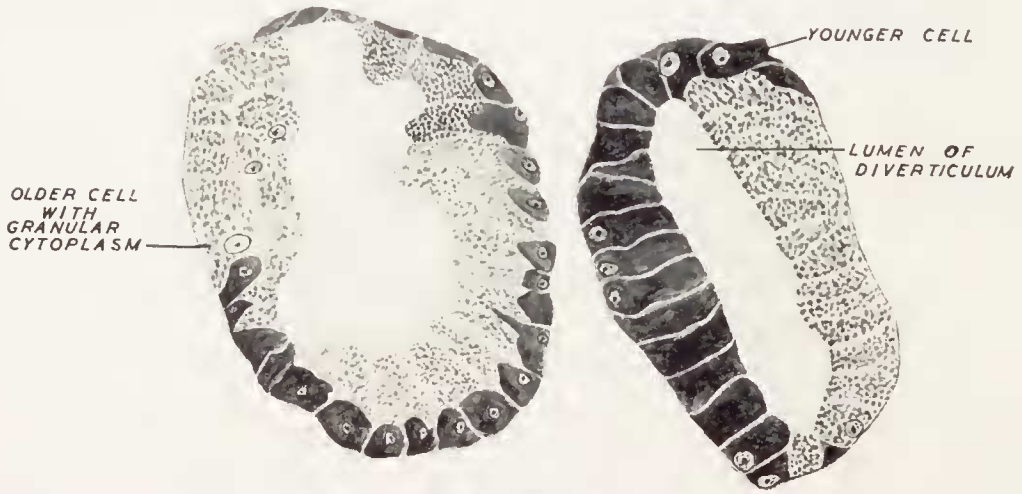

FIG. 3- T.S. DIGESTIVE DIVERTICULAE X700 (*K. SCALARINA*)

The diverticulae are connected to the ducts by short narrow tubules lined with short ciliated columnar epithelial cells similar to those found in the stomach and the ducts. The tubules enter the ducts separately. The later have, in cross section, an irregularly shaped lumen, possibly due to variation in the size of the epithelial cells.

The vertical limb of the intestine which leaves the stomach at its posterior end consists of two compartments partially separated from each other by two ridges or typhlosoles. The large compartment is the style sac, the smaller the intestinal groove.

The epithelia lining these two compartments differ although they are both composed of a single layer of ciliated columnar epithelial cells. Those of the style sac are tall with large oval nuclei, having a prominent nucleolus and a faint network of chromatin, and situated in the lower half of the cell. The cilia are long, straight and very numerous arising from a row of basal granules near the outer border of the cells. The most noticeable feature of the cilia is that they are all the same length, the style resting on the surface so formed. (Fig. 4.)

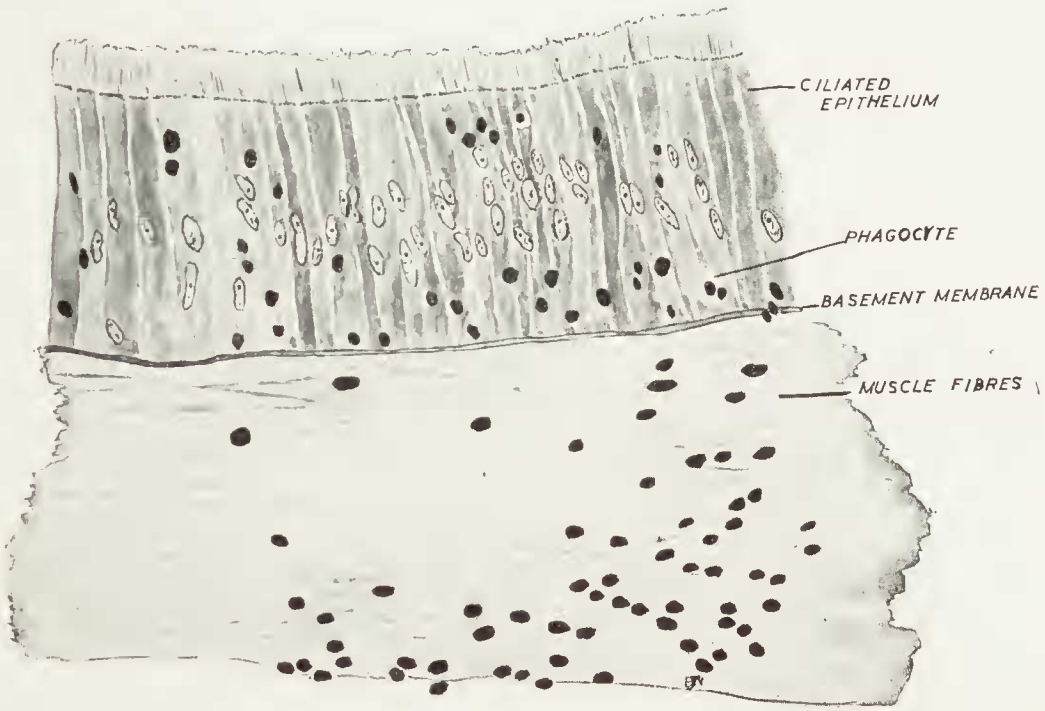

FIG. 4 - T.S. WALL OF MID GUT, STYLE SAC X 700
(*K. SCALARINA*)

At the typhlosoles the nature of the cilia changes, and the cells lining the intestinal groove are shorter, the cilia sparser and less uniform. The left typhlosole is the larger, projecting further into the lumen. It consists of a thickening of the underlying connective tissue and muscle covered by ciliated

columnar epithelial cells similar to those of the intestinal groove. The smaller right typhlosole is formed by a group of very tall columnar epithelial cells, supported to some extent by a slight thickening of the underlying tissues. A few of these tall cells are seen on the posterior surface of the left typhlosole.

It is interesting to note that the relation of the style sac to the intestinal groove is very similar to that shown by Matthais (1914, Fig. 77) for *Arca barbata,* rather than to that of *Ostrea edulis* (Yonge, 1926B) or that of *Anodonta cellensis* (Gutheil, 1912) and *Anodonta grandis, Lampsilis luteolus* and *Lampsilis anodontoides* (Nelson, 1918). Systematically these latter forms are more closely related to *Katelysia scalarina* than is *Arca barbata.*

Phagocytes are very numerous both in and beneath the epithelium of the intestinal groove and were less numerous in the epithelium of the style sac. Some of the phagocytes, especially those near the typhlosoles contain large brown-green granules about 0·0078 mm. in diameter. These granules are spherical in shape and occur throughout the body of the animal particularly in the intenstinal epithelium, in the blood vessels and the renal organ. MacMunn (1900) maintains that they are composed of a substance related to chlorophyll and called by him entero-chlorophyll. He believes it to be a derivative of ingested chlorophyll. Zachs (1955) in a paper on the cytochemistry of *Venus mercenaria* has summarized the past observations on this pigment and has shown for *V. mercenaria* that this pigment is allied to ceroid, a substance produced during the cirrhosis of rat's liver and first described by Lillie and his co-workers (1941, 1942). Prior to this, several workers, Metchnikoff (1884), Grobben (1887) and Yonge (1926 A and B) had observed these pigment masses in various organs of molluscs. In lamellibranchs they occur primarily in the blood vessels and tissues of the digestive gland, intestine, heart and kidney.

The crystalline style has not been studied in detail as it was not directly related to the subject and much has already been done on this aspect of molluscan anatomy (Nelson, 1918). Although the style was not dissected out, it was seen in a section cut through the stomach and appeared as a more or less homogenous translucent mass. The style sac ends just after the coiling of the intestine and the intestine continues as the mid gut.

The mid gut is characterized by a large typhlosole occupying the greater part of the lumen of the gut. Unlike that described by Yonge (1926) for *Ostrea edulis,* the typhlosole is not bilobed. It is composed mainly of connective tissue and some muscle fibres, the latter tending to be concentrated in the centre of the typhlosole. Scattered throughout the connective tissue are numerous phagocytes.

The epithelium of the mid gut is composed of columnar cells similar to those lining the stomach although the cilia are longer, being nearly half the length of the cell. The cells rest on a very thick basement membrane which is underlain by a layer of circular muscle in the typhlosole. Through the epithelium, basement membrane and muscle layer there are numerous phagocytes, many containing large inclusions of the brown-green ceroid-like excretory pigment. (Fig. 5.)

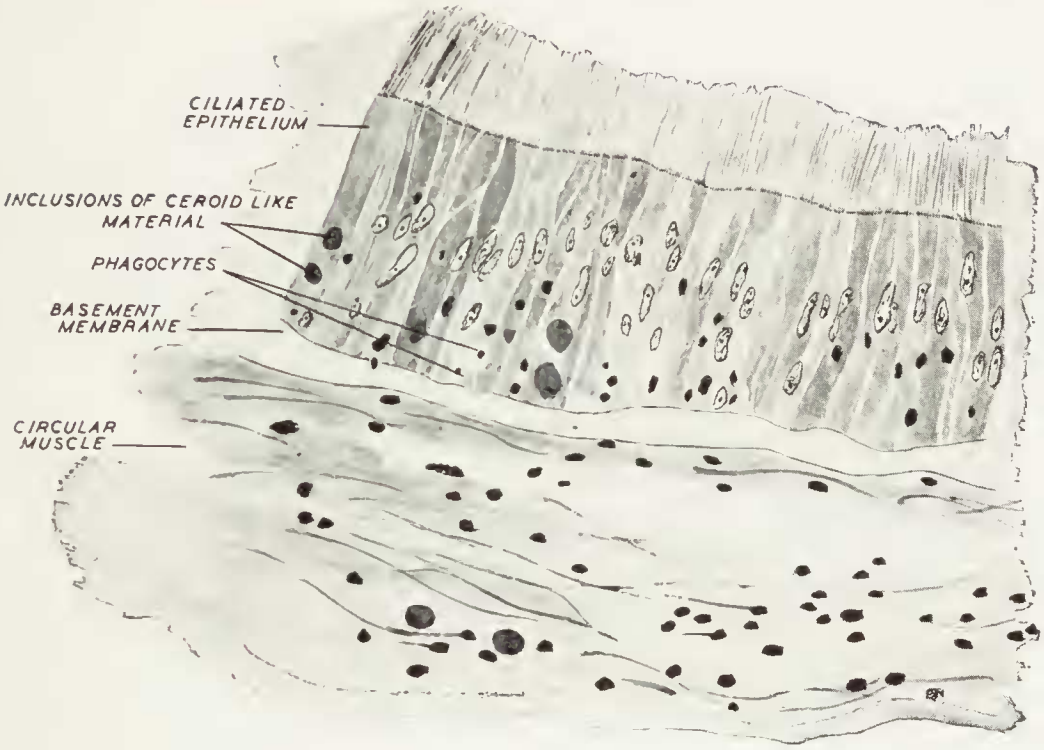

FIG. 5 - T.S. WALL OF MID GUT, TYPHLOSOLE. X 700
(*K. SCALARINA*)

The rectum is circular in cross section and the lumen is likewise. There is no evidence of a typhlosole anywhere, the lumen being lined by columnar cells with short cilia. Here the phagocytes are even more numerous, occurring both in the epithelium and the lumen of the rectum, many containing brown granules. There is a very narrow basement membrane surrounded by a thick layer of circular muscle.

Vascular System:

The heart lies in the pericardial cavity which is dorsal, lying immediately anterior to the posterior adductor muscle and is similar to most lamellibranch hearts (White, 1928). It consists of a ventricle and a pair of auricles. The ventricle has thick spongy muscular walls while the auricles, opening into either side of the ventricle by narrow transverse slits, have thin transparent walls. The rectum passes through the ventricle.

The arterial system was traced by injecting a suspension of red poster paint in sea water into the ventricle, the method used being a modification of that used by Awati and Rae for *Ostrea cucullata*. The arteries were subsequently dissected. Most of the main arteries were clearly revealed by this method but the pedal artery was filled only in one specimen and those to the mantle and siphons did not fill at all. (Fig. 6.)

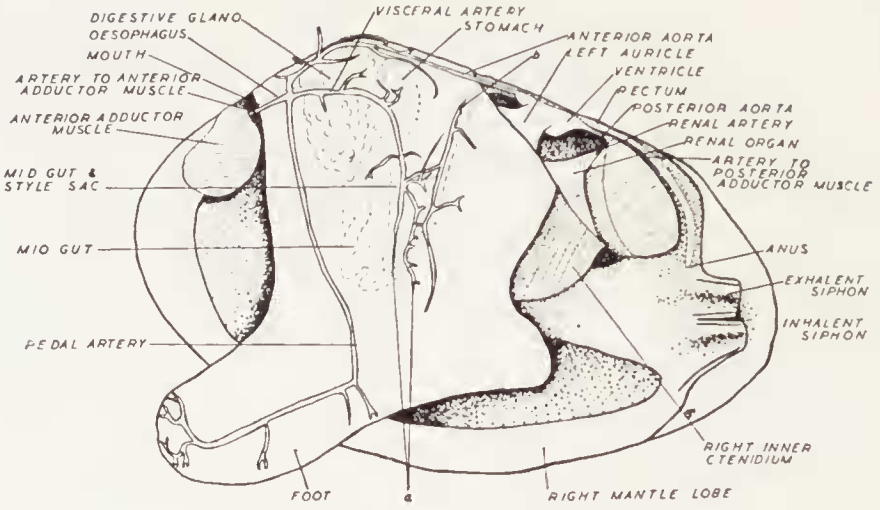

FIG 6-ARTERIAL SYSTEM, *K SCALARINA*

From the ventricle two main arteries arise, the anterior and posterior aortae. The anterior aorta leaves the ventricle on the dorsal side of the rectum and runs along the dorsal surfaces of the rectum until it enters the visceral mass. From here it continues along the dorsal side of the visceral mass just below the body epithelium giving off several small branches to the surrounding tissues and to the rectum. It passes dorsal to the digestive gland and on the anterior side of this organ turns in a ventral direction dividing into three branches—one to the anterior adductor muscle; one to the foot, the pedal artery; and one to the viscera, the visceral artery.

The artery to the anterior adductor muscle is short and enters the muscle immediately after leaving the visceral mass. The pedal artery runs parallel to the anterior margin of the visceral mass until it reaches the foot where it runs parallel to the ventral margin of the foot and after giving off several small branches finally divides into small vessels at the tip of the foot.

The visceral artery is a large artery which passes posteriorly through the digestive gland, giving off branches to the stomach and digestive gland. It then travels down the style sac dividing into four branches about halfway along the style sac. One of these branches is very short serving the surrounding gonads while the other three extend over the alimentary canal bringing blood to the mid gut and rectum.

The posterior aorta runs along the ventral surface of the rectum giving one branch to the renal organ before entering the posterior adductor muscle. Halfway between the ventricle and the renal artery there is a curious outgrowth on the ventral aorta, the aortic bulb, the function of which is unknown.

Owing to difficulty in determining a suitable point of injection the venous system has not been investigated.

Nervous System:

The nervous system of the two species is essentially the same and a full description will be found in the description of *K. rhytiphora*.

Ctenidia:

The ctenidia are strongly plicate and the central plicae of the inner demibranch average 26 filaments to each plica. The filaments are typical of the Eulamellibranchiata and are similar to those of *Venus callophylla* illustrated by Ridewood (1903). There are no principal filaments.

The ciliation of the ctenidia was not studied as attempts at determining the direction of the food currents proved unsuccessful. Two methods were tried, that described by Atkins (1936, 1937 A and B, 1938 and 1943) and that used by MacGinitie (1941, 1945).

Katelysia rhytiphora Lamy, 1935.

Venus corrugata Lamarck 1818 (non Gmelin) (p. 594, No. 34).

Venus aphrodina Lamarck 1818 as described by Hanley 1842, 1856 (p. 126, pl. 16, fig. 33).

Venus strigosa Sowerby 1855 (p. 736, No. 99, pl. 162, fig. 222, 223); Reeve 1864 (pl. 20, sp. 94) (non Lamarck 1818).

Chione strigosa Pritchard and Gatliff 1903 (p. 126, p. 94, pl. 15, fig. 5, 6).

Tapes victoriae Pritchard and Gatliff 1903 (p. 126) (non Tenison Woods 1878).

Marcia (Katelysia) corrugata Jukes-Brown 1914 (p. 88).

Marcia corrugata May 1921, 1923 (p. 23, No. 176, pl. 10, fig. 13).

Katelysia enigma Iredale 1936 (p. 278); Allan 1950 (p. 331, p. 326, fig. 77, No. 8).

Katelysia strigosa Macpherson and Chapple 1951 (p. 152).

Katelysia rhytiphora Macpherson 1958 (p. 14, pl. 10, No. 13).

Shell:

Shell equivalve, inequilateral, anterior dorsal margin more than half the length of the posterior dorsal margin. The angle at the umbos between the two dorsal margins averages 131 deg. The ventral margin is smooth flatly convex; the posterior and anterior margins are rounded. The hinge line is typical of the family with three cardinal teeth in each valve—$\frac{\text{L } 101010}{\text{R } 010101}$; there are no laterals. The central cardinal tooth in both valves is very slightly bifid and extends to the edge of the hinge plate. The two outside cardinals are set at equal acute angles to the central tooth and all tend to be slightly curved. The ligament is external and typical of the family. The lunule is lanceolate well defined but darker in colour than the rest of the shell. The escutcheon is narrow and inconspicuous. The shell sculpture consists of concentric rounded coarse ridges tending to unite towards the posterior margin. These ridges are crossed by coarse radial costae which are characteristic of the species. Internally the adductor muscle scars and the pallial line are pronounced, the pallial sinus being moderately deep and wide.

The outside of the shell is cream with black angular markings covering most of the shell, while the inside is yellow with purple about the anterior and posterior dorsal margins and also the adductor muscle scars. In some forms such as those from Port Arthur, Tasmania the whole interior is deep purple.

The variation within this species is not as great as that in the previous species. Shells from New South Wales, both recent and sub-recent, are in general more swollen than the Victorian form, particularly towards the umbos and the radial costae are very close together. This form seems to be restricted to the east coast of New South Wales being recorded as far south as Eden. The Victorian form of the species is similar to that of the type but changes occurring as the species is followed east and west are not sufficiently marked to warrant further sub-division of the species.

Most of the specimens seen from South Australia were from St. Vincent's Gulf, particularly about Adelaide. The valves are flatter, the concentric ridges broader and stronger and the radial costae coarser. Specimens from Eyre Island were shorter anteriorly resulting in the anterior dorsal and posterior dorsal margins being almost equal in length.

The species is rare in Western Australia. Specimens from here differ from the Victorian forms in that the concentric ridges are broader, the external surface more polished and the posterior end more pointed. The external colouration also varies although basically typical of the species. The shells are lighter in colour and often the posterior end of the shell is brown. In the shells from Port Arthur, Tasmania the central cardinal tooth in the left valve is often strongly bifurcated and the valves shorter dorsoventrally, often thick. The colouration varies considerably, from that of the type to the deep purple inside and grey-green outside, common to all species at Port Arthur.

Distribution:

The range of *K. rhytiphora* is similar to that of *K. scalarina*. (Fig. 7.) In New South Wales it is not recorded further north than Sydney, occurring there mainly as sub-recent valves washed up on the beach. The only other record from New South Wales is a live specimen from near Eden.

In Victoria the species is plentiful particularly in Port Phillip and also in some localities of Western Port. It is also found in the more sheltered inlets, bays and gulfs of the South Australian coast particularly St. Vincent's Gulf. It occurs in the Pleistocene deposits of this state although Crocker and Cotton did not record it. In a deposit five miles west of Lake St. Claire, mentioned earlier, *K. rhytiphora* is more common than *K. scalarina*.

FIG 7 - DISTRIBUTION OF K RHYTIPHORA & K.PERONII

The species is not common in Western Australia and has been recorded only from one locality, Emu Point near Albany. In Tasmania the distribution of this species is slightly different from that of the former species. *K. rhytiphora* seems to be more restricted to the southern coast while *K. scalarina* occurs both on the northern and southern portions of the coast.

Ecology:

The habitat of this species is different from that of *K. scalarina* although there is a slight overlap. Of the localities visited by the writer, Mornington is the only one where both species are found. Here, as mentioned above, *K. scalarina* is found between the tide marks while below the lower limits of this band, *K. rhytiphora* occur often buried in the *Zostera,* a few living among the *K. scalarina.*

At Flinders, Western Port, *K. rhytiphora* is found buried in a grey muddy sand near banks of *Zostera* on the north west side of West Head, just north of the end of the basalt wave platform at the base of West Head. Here they are uncovered only at low spring tides, the only other bivalve associated with them being *Zemyria tasmanica.*

Another locality visited by the writer was Geelong where the *K. rhytiphora* were living well below low tide in about a metre of water. Here again they were buried in a muddy sand, this time associated with *Eumarcia fumigata* and *Philine angasi,* the latter being quite plentiful.

Occasionally when *K. rhytiphora* is the only member of the genus in the locality, as for example at Rickett's Point, Port Phillip, a few individuals are found between the tide marks, often being detected by a growth of *Ulva lactucea* on the posterior end of the shell. The commensal sea-anemone associated with *K. scalarina* does not occur on *K. rhytiphora* even when the two species are closely associated as they are at Mornington.

Animal Morphology.

The external morphology of the animal of *K. rhytiphora* does not differ greatly from that of *K. scalarina.* The epithelium lining the inside of the siphons lacks the black pigment found in *K. scalarina.* The foot is similar in shape to that of *K. scalarina* although it is shorter in the dorsal ventral direction and longer in the anterior-posterior direction. The external aperture of the exhalent siphon is similar to that of *K. scalarina* (Fig. 8).

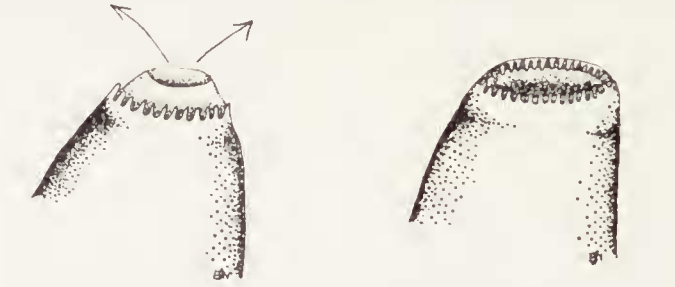

FIG. 8 - EXHALENT SIPHON X 1 2
(*K. RHYTIPHORA*)

ANATOMY AND HISTOLOGY.

Alimentary Canal and Associated Organs:

The alimentary canal does not differ greatly from that of *K. scalarina* and will not be described.

Vascular System:

In general plan the heart and arterial system are similar to that of *K. scalarina.* There are some differences in the arterial system and these will be described in detail.

The arterial system was traced in the same way as that of *K. scalarina.* Unfortunately while most of the main arteries were revealed in this species, those of the foot and mantle did not fill with the injected material. It is assumed that the pedal artery takes a similar course to that of *K. scalarina.* (Fig. 9.)

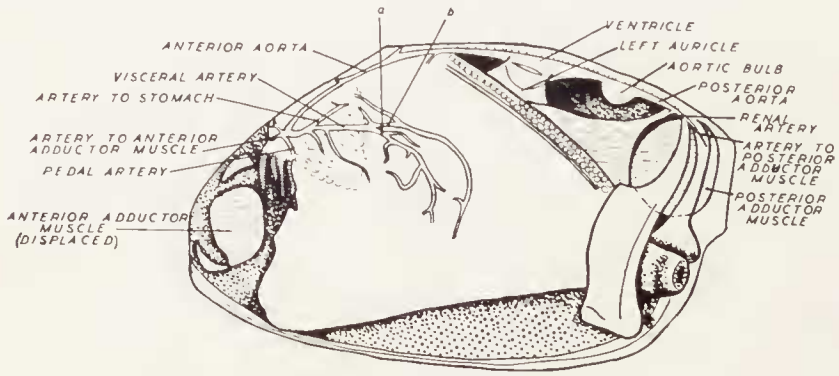

FIG. 9 - ARTERIAL SYSTEM, *K RHYTIPHORA*

The anterior aorta after it passes through the digestive gland gives off two important branches, the artery to the stomach and the larger visceral artery which takes blood to the intestine. This visceral artery has two main branches which correspond to *a* and *b* in Schanecke's description of the arterial system of *Anodonta cellensis* (Schanecke, 1913). Branch *a* of the visceral artery serves the coiled portion of the intestine lying in the ventral part of the visceral cavity as well as giving off numerous small branches to the surrounding tissues including the gonads and the body wall. Branch *b* of this artery immediately divides into two, one branch passing dorsally to take blood to the stomach and also the dorsal ascending posterior portion of the intestine. The other branch extends ventrally serving the ventral ascending portion of the intestine and the coiled intestine. Anterior to the junction of branches *a* and *b* the visceral artery gives off three branches two of which serve the digestive gland, the third passing through this gland into the gonads surrounding the digestive gland.

Nervous System.

The dissection of the nervous system was made on animals fixed in Müller's fluid. The advantage of this fixative over formalin is that the ganglia particularly and also the nerves to a lesser extent take up the orange potassium dichromate and are easily distinguished against the white of the muscles. Also the tissues are not distorted during fixation. A disadvantage is that fixation is very slow, the time used for *K. rhytiphora* being about the minimum.

The nervous system was compared with that of *Tagelus dunbeyi* (Solenidae) and *Pholas dactylus* (Pholadidae) described by Haas (1935, Fig. 503 and 505, p. 878 and 879) Stempel (1912) and Forster (1914). In general it is more like that of *Pholas dactylus* (L) and most of the names for the nerves have been taken from Forster (1914).

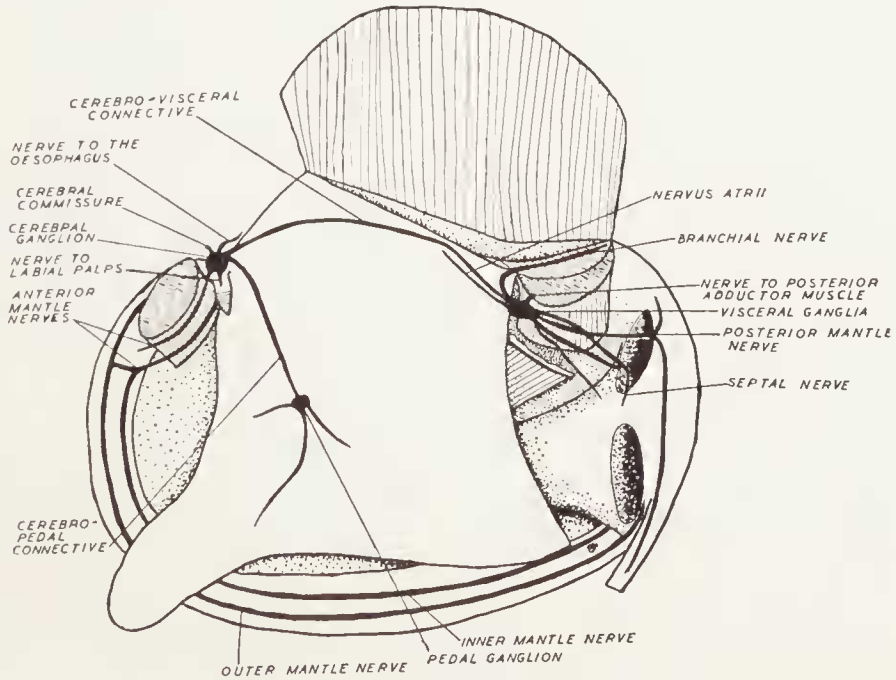

FIG 10 - NERVOUS SYSTEM, *K RHYTIPHORA*

Ctenidia:

The structure of the ctenidia is similar to that of *K. scalarina*. However, the central plicae of the inner demibranch average 21 filaments to each plica compared with 26 in *K. scalarina*.

Mantle Edge and Siphons:

The morphology of the mantle edge and siphons has been described already. The histology of these organs has been considered in the light of Yonge's note (1948) in which he gives the structure of the mantle and postulates the fusion of the lobes to give the siphons. It was decided to section both mantle edge and siphons to see if, in fact, these three divisions of the mantle edge were distinguishable histologically. The diagram given by Yonge is very generalized and seems to indicate that the radial muscles only extend from the inner lobe to the pallial line but in *Katelysia* some extend from the outer lobe (that is, the lobe applied closely to the shell) to the pallial line so that both the inner and outer lobes are muscular.

Likewise the presence of a middle sensory lobe is open to question as there does not seem to be a particular concentration of nervous tissue in this lobe. As can be seen from Fig. 10 there are two mantle nerves on which there are occasional small ganglia. Nerves from these ganglia serve the tentacles and muscles of the mantle edge.

Sections through the siphons show that there are giant nerve fibres in the nerves to the siphons from the visceral ganglia.

Pedal Gland:

Along the ventral edge of the foot there is a ciliated groove extending from the centre of the foot in an anterior direction for about 6–7 mm. This groove contains at its posterior end the pedal gland which corresponds with the byssal gland of sessile forms such as *Mytilus*, *Arca* and *Pinctada*. There is no evidence of a byssus in *Katelysia*. Sections through the gland show that the cells forming it are columnar with a prominent, darkly staining nucleus. The cytoplasm of the cells is packed with golden brown granules. The nature of these granules is unknown although they do not appear to resemble the ceroid material observed in other parts of the body. Both species have this gland and groove.

Statistical analysis of shell measurements of *K. scalarina* and *K. rhytiphora*.

A statistical analysis of five shell measurements was made on 331 specimens of *K. scalarina* and 359 specimens of *K. rhytiphora* in order to determine whether there was a constant difference in the form of the shell.

The measurements made were: —

I. Length of shell (anterior to posterior).
II. Distance from posterior edge to umbos.
III. Distance from anterior edge to umbos.
IV. Width (Left to right).
V. Angle at umbos.

The three principal ganglia are paired. Usually members of a pair are closely applied to one another. However the cerebral ganglia are found one on either side of the oesophagus just posterior to the mouth and are connected to each other by the cerebral connective dorsal to the oesophagus. (Fig. 10.)

The cerebral ganglia are connected by paired cerebro-pedal connectives to the pedal ganglia which lie in the muscular body wall just anterior to the visceral cavity and about half-way between the dorsal and ventral margins of the body. The cerebral ganglia are also connected to the visceral ganglia by the paired cerebro-visceral connectives which run on either side of the body, just below the thin muscular body wall covering the digestive gland. Just posterior to the genital aperture this connective passes through the renal organ, running along its ventral margin until the connective joins the visceral ganglia. Other nerves, the anterior mantle nerves, leave the anterior side of the cerebral ganglia and after passing over the posterior surface of the anterior adductor muscle, branch into the inner and outer mantle nerves serving the mantle edge. There are two other pairs of shorter nerves leaving the cerebral ganglia. One pair is dorsal and innervates the oesophagus. The other pair is ventral, the nerve origins lying between those of the anterior mantle nerve and the cerebro-pedal connectives. This pair innervates the labial palps.

The pedal ganglia give rise to three pairs of nerves, one passing anterior into the body wall, another ventrally to the foot and a third posteriorly to the intestine. There does not appear to be pairs of statocysts associated with the pedal ganglia, as recorded in some forms such as *Nucula nucleus* (L) (Pelseneer, 1891) and *Spondylus* (Dakin, 1928) but these may be undetected due to small size.

The visceral ganglia are conspicuous lying in the connective tissue covering the ventral surface of the adductor muscle. Just ventral to the origin of the cerebro-visceral connective there is a small nerve which seems to correspond to the nervus atrii of Stempell (1912). Dorsal to the origin of the cerebro-visceral connective the branchial nerves leave the visceral ganglia and pass across through connective tissue onto the inner dorsal side of the inner gill ctenidium and there turn posteriorly to the gill margin.

A pair of short nerves leaves the dorsal side of the visceral ganglia and passes straight into the posterior adductor muscle. Posteriorly two pairs of nerves leave the ganglia. One pair, the posterior mantle nerves, passes over the ventral surface of the posterior adductor muscle and through the connective tissue about the inner aperture of the exhalent siphon to the mantle where each nerve divides in two, a branch passing to the dorsal portion of the mantle, another ventrally to join with the outer mantle nerve from the anterior mantle nerve. The other pairs of nerves each lie to the outside of the posterior mantle nerves and cross the latter before entering the septum between the inner aperture of the two siphons. These nerves seem to correspond to the septal nerves of Forster (1914) and pass up the siphon walls innervating the siphons. It is not certain whether a branch from this nerve also joins with the inner mantle nerve of the anterior mantle nerve.

The histology of the nervous system has not been studied in detail although in a series of sections through the whole animal the gross structure of the cerebral ganglia was revealed. Most of the nerve cells seem to be concentrated in the outer portion of the ganglia while the central region consists of a vast network of axons leading into the nerves serving the various organs.

The results of this analysis may be summarized as follows:—

	K. scalarina.	*K. rhytiphora.*
I. Length—		
Mean	28·30 ± 0·31 mm.	31·93 ± 0·41 mm.
Standard Deviation	5·71 mm.	7·73 mm.
II. Posterior edge-umbos—		
Mean	25·88 ± 0·29 mm.	26·92 ± 0·35 mm.
Standard Deviation	5·35 mm.	6·64 mm.
III. Anterior edge-umbos—		
Mean	11·84 ± 0·13 mm.	12·90 ± 0·16 mm.
Standard Deviation	2·28 mm.	3·02 mm.
IV. Width—		
Mean	12·61 ± 0·14 mm.	13·84 ± 0·20 mm.
Standard Deviation	2·58 mm.	3·78 mm.
V. Angle at umbos—		
Mean	114·38 ± 0·42°	131·57 ± 0·27°
Standard Deviation	7·57°	5·17°

ANALYSIS OF THE DIFFERENCE BETWEEN THE TWO SAMPLES.

(*a*) *Comparison of Means.*

As a simple rule it can be stated that two samples are probably different if the difference between the means ($m_1 - m_2$) is more than twice the sum of the standard errors ($SEm_1 + SEm_2$) and almost certainly different if it is more than three times the sum of the standard errors. (Mayr, Lindsley and Usinger, 1953).

The fraction $\frac{\text{Difference between means}}{\text{Sum of SEm}}$ gives the following figures:—

I. Length	5·1
II. Posterior edge-umbos	1·6
III. Anterior edge-umbos	3·6
IV. Width	3·6
V. Angle at the umbos	24·9

Since four of the five measurements made show a difference between the means which is greater than three times the sum of the standard errors, the samples are almost certainly from different populations.

(*b*) *Overlap of Population.*

Using the coefficient of difference (C.D.) as defined by Mayr, Lindsley and Usinger (p. 145–146) the following results were obtained:—

	C. D.	Joint Non-overlap.
I. Length	0·3	Less than 75 per cent.
II. Posterior edge-umbos	0·1	Less than 75 per cent.
III. Anterior edge-umbos	0·2	Less than 75 per cent.
IV. Width	0·2	Less than 75 per cent.
V. Angle	1·35	91 per cent.

A further study of the results of the first two measurements taken as $\frac{\text{Posterior edge-umbos}}{\text{Length}} \times 100$ gave the following:—

VI. $\frac{\text{Posterior edge-umbos}}{\text{Length.}}$	1·19	88·5 per cent.

From these results it can be seen that the angle at the umbos may be used as a character for distinguishing the two species.

Breeding in *Katelysia scalarina* and *Katelysia rhytiphora*.

In order to determine the breeding cycles of the two species a monthly survey of the population at Mornington was started in September, 1955 and continued more or less regularly for *K. scalarina* up to the beginning of October, 1956. Unfortunately the number of *K. rhytiphora* available was not great and after June, 1956, gave out completely. Apart from the original aim of this survey it has been possible to consider the type of sexuality present in the species and in November, 1955 to carry out experiments in cross fertilization between the two species.

As in most lamellibranchs the gonad in both sexes consists of a vast network of ramifying tubes eventually forming a common duct which opens to the exterior onto a small genital papilla just near the anterior end of the renal organ. The gonads are paired and at maturity completely fill every available space in the body cavity, covering the intestine and digestive gland, and extending right up into the umbos of the shell causing considerable extension of the body wall. They do not extend into the mantle as in *Mytilus*.

There is little apparent macroscopic difference between the two sexes. Unlike *Spondylus, Pecten* and *Chlamys* there is no difference in the colour of the gonad; in both species it is pale cream. However, there is a slight difference in the texture of the gonad apparent through the body wall particularly in mature specimens. In the female the tubules of the gonad are distinct while those of the male are suffuse and tightly packed. There is no difference in the shells of the two sexes as in some members of the family *Carditiidae* (Dall, 1902).

Unlike many of the *Ostreidae* the larvae are not retained within the mantle cavity. The genital products are discharged into the sea where fertilization occurs. At present the length of the larval period is unknown, as are the larval stages.

During this survey one hundred specimens of *K. scalarina* were collected on each visit to Mornington, as well as any *K. rhytiphora* available. They were preserved in 5 per cent. formalin. Subsequently the length of each shell was determined, the animal sexed by microscopical examination of gonad smears and the developmental stage of the gonad estimated. This last part was done by devising an arbitrary series of developmental stages similar to that used by Orton, Southward and Dodd (1956) for *Patella vulgata*. These stages were as follows:—

	Stage Number.	Condition of Gonad.
Prior to Spawning	1.	Body cavity empty of genital products (includes immature individuals).
	2.	Body cavity partly full—digestive gland completely uncovered.
	3.	Body cavity partially full—portion of digestive gland still showing.
	4.	Body cavity full but not strongly distended—digestive gland completely covered.
Spawning commences.	5.	Body cavity packed with mature products, body wall strongly distended and hard to the touch.
Spawning and post spawning.	IV.	One gonad half empty.
	III.	Both gonads half empty.
	II.	Both gonads almost fully discharged.
	I.	Both gonads empty—body wall loose.

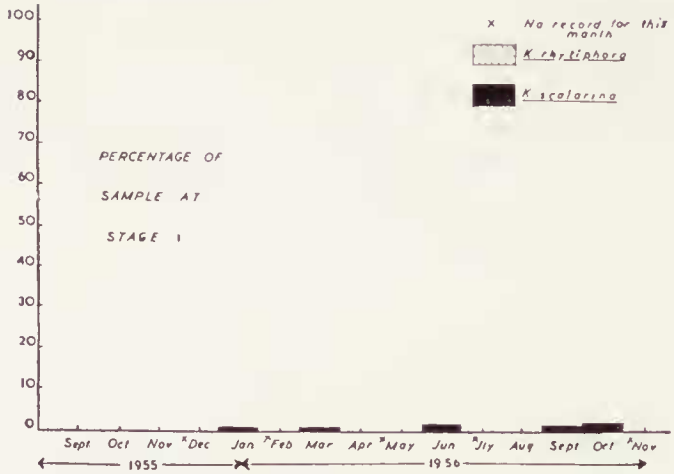
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE 1
X No record for this month
K. phrygiphora
K. scalarina
Sept. Oct. Nov. R Dec. Jan. R Feb. Mar. Apr. R May. Jun. R Jly. Aug. Sept. Oct. R Nov.
1955
1956

FIG. 11

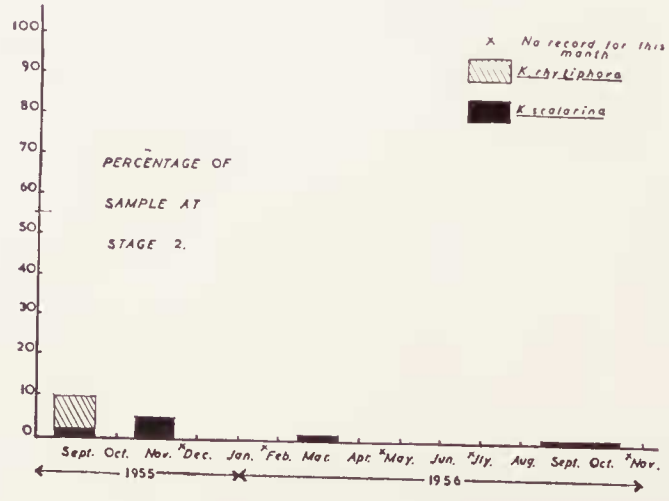
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE 2.
X No record for this month
K. phrygiphora
K. scalarina
Sept. Oct. Nov. R Dec. Jan. R Feb. Mar. Apr. R May. Jun. R Jly. Aug. Sept. Oct. R Nov.
1955
1956

FIG. 12

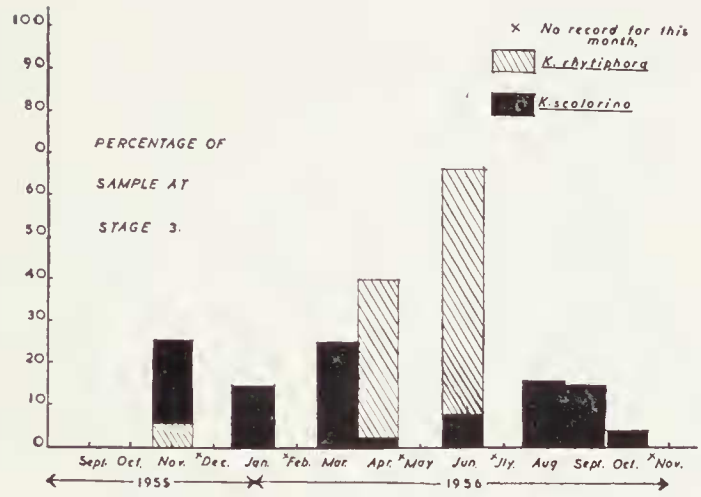
100
90
80
0
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE 3.
× No record for this month.
K. rhytiphora
K. scalorino
Sept. Oct. Nov. *Dec. Jan. *Feb. Mar. Apr. *May Jun. *Jly. Aug Sept. Oct. *Nov.
1955
1956

FIG. 13

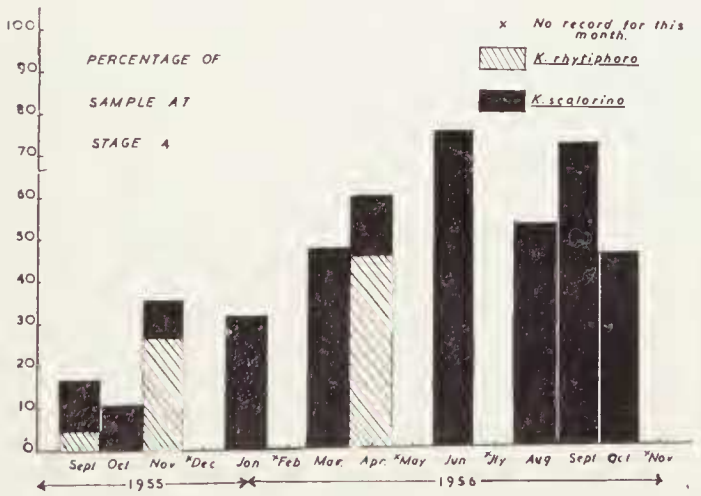
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE 4
× No record for this month.
K. rhytiphora
K. scalorino
Sept Oct Nov *Dec Jan *Feb Mar Apr *May Jun *Jly Aug Sept Oct *Nov
1955
1956

FIG. 14

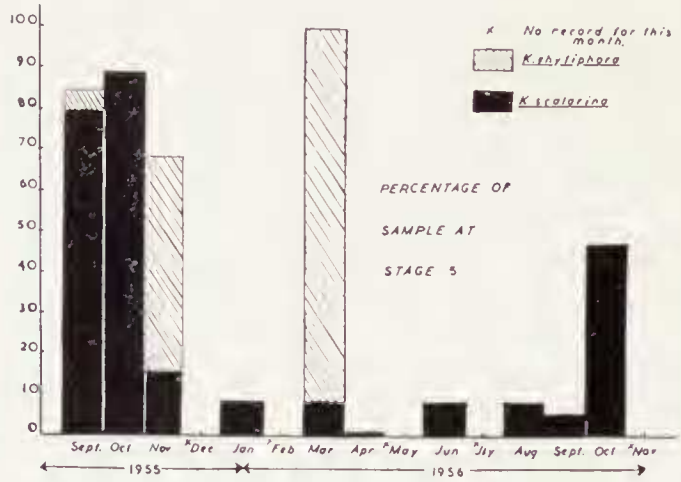
100
90
80
70
60
50
40
30
20
10
0
x No record for this month.
K rhytiphora
K scalorina
PERCENTAGE OF
SAMPLE AT
STAGE 5
Sept. Oct. Nov. xDec. Jan. xFeb. Mar. Apr. xMay Jun. xJly. Aug. Sept. Oct. xNov.
1955
1956

FIG 15

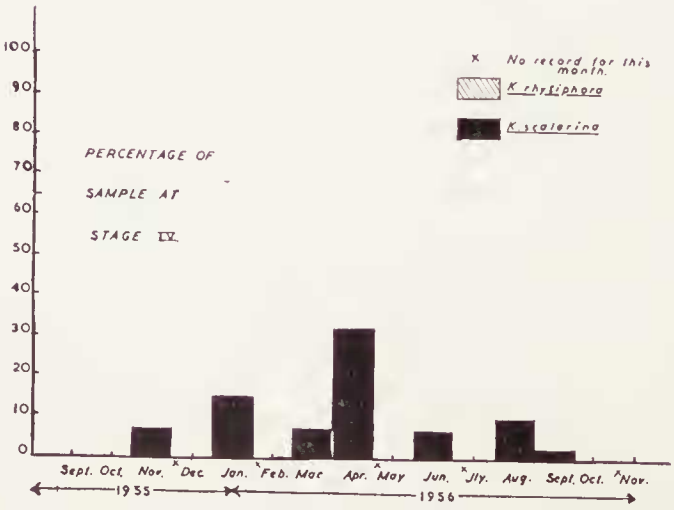
100
90
80
70
60
50
40
30
20
10
0
x No record for this month.
K rhytiphora
K scalorina
PERCENTAGE OF
SAMPLE AT
STAGE IV
Sept. Oct. Nov. x Dec. Jan. x Feb. Mar. Apr. x May Jun. x Jly. Aug. Sept. Oct. x Nov.
1955
1956

FIG. 16

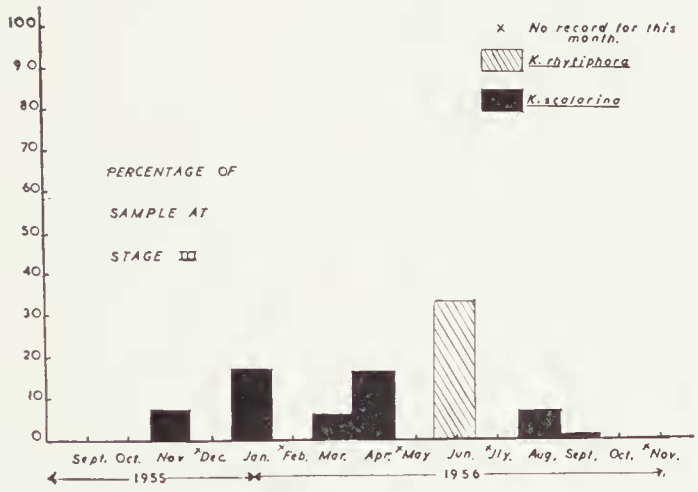
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE III
x No record for this month.
K. rhytiphora
K. scalarina
Sept. Oct. Nov. *Dec. Jan. *Feb. Mar. Apr. *May Jun. *Jly. Aug. Sept. Oct. *Nov.
1955
1956

FIG. 17

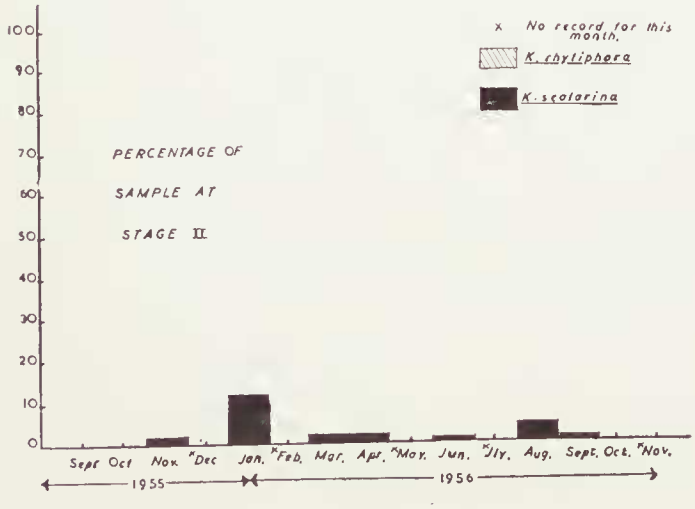
100
90
80
70
60
50
40
30
20
10
0
PERCENTAGE OF
SAMPLE AT
STAGE II
x No record for this month.
K. rhytiphora
K. scalarina
Sept. Oct. Nov. *Dec. Jan. *Feb. Mar. Apr. *May. Jun. *Jly. Aug. Sept. Oct. *Nov.
1955
1956

FIG. 18

A certain amount of difficulty was experienced in distinguishing stages 4 and IV., but usually spawning animals could be distinguished by the fact that the body wall was flaccid and one or both gonads half empty. The condition of the body was used as a criterion in all the spawning and post spawning stages. Figures 11 to 19 show the results of this survey.

Figure 15 shows that the main spawning period for *K. scalarina* is in September–October, maturity being reached slightly later in 1956. There is a possibility that another secondary spawning period may occur in March particularly for *K. rhytiphora*. In fact there appears to be no time at which the gonads of the whole population are resting, i.e. in stages 1 or I. This indicates that there is no indeterminate period between the breeding seasons when the gonad is reduced and no genital products appear in sections. (Figures 11 and 19.) This "indeterminate" period has been recorded by Orton and his co-workers (1956) in *Patella vulgata* and also by Loosanoff (1942) in *Ostrea virginica*. Both these species are ambisexual and are described by Coe (1943, 1944) as exhibiting alternate sexuality. The absence of the "indeterminate" period in *K. scalarina* suggests that this species may not exhibit alternate sexuality although the presence of ambisexual individuals suggests that another type of ambisexuality could be present.

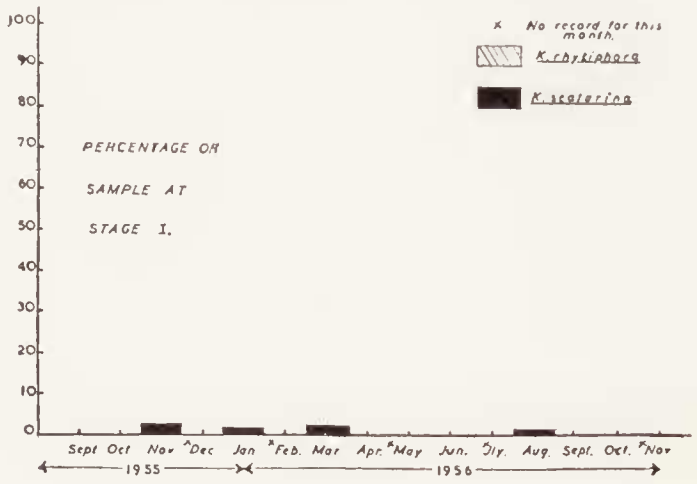

FIG. 19

Although no young individuals were obtained at Mornington Miss J. H. Macpherson of the National Museum of Victoria made available a collection from Venus Bay, South Australia collected on the 12th February, 1956. The shells of these animals averaged 18 mm. long. Of the 40 specimens collected, 15 were immature showing no gonad and of the 25 with gonad developed 9 were males and 16 females. This suggests that the species is not protandric as is *Venus mercenaria* Loosanoff (1937) where 98 per cent. of the population studied was protandric. However further work must be done before any definite conclusion can be reached.

As mentioned earlier the number of *K. rhytiphora* collected was relatively small. Despite this there are indications that the spawning periods are similar to those of *K. scalarina*. September, November and March appeared to be the main spawning periods.

Samples from the population of *K. scalarina* obtained each month showed that it consisted of male, female and ambisexual individuals.

The size range within the sexes was calculated. Of the total number of individuals collected, namely 993, 41·9 per cent. were female, 50·5 per cent. were male and 7·6 per cent. ambisexual. The mean size of the males was 30·4 mm. and that of the females 30·9 mm. Assuming that the length of the shell is directly proportional to age, these figures indicate that the individuals of each sex were approximately the same age. This again eliminates the possibility of ambisexuality being the dominant type of sexuality.

The proportion of male, female and ambisexual individuals was roughly the same for the 58 individuals of *K. rhytiphora* collected. Of these, 50 per cent. were female, 46·6 per cent. male and 3·4 per cent. ambisexual. The mean length of the males is 33·6 mm. and that of the females 33·8 mm. Thus the conclusions applied above to *K. scalarina* may also be applied to this species.

Perhaps the most interesting part of this work was the cross fertilization experiment carried out on the 10th November, 1955. For this experiment *K. scalarina* were collected at Mornington and *K. rhytiphora* at Ricketts Point. The animals were sexed and suspensions of ova and sperm of both species were made in sea water. After some time four separate crosses were made which were as follows:

Cross.	Sperm.	Ova.
1	*K. scalarina*	*K. scalarina*
2	*K. scalarina*	*K. rhytiphora*
3	*K. rhytiphora*	*K. scalarina*
4	*K. rhytiphora*	*K. rhytiphora*

Of these four crosses, Nos. 1 and 4 acted as controls while Nos. 2 and 3 were made to determine whether it was possible for cross fertilization to occur between the two species in the one locality.

After a time the ova in each cross were examined microscopically. Those from crosses 1 and 4 appeared the same, sperm being clustered about the periphery of each ovum. About half an hour later the first polar body was seen to form and the unsuccessful sperm disperse.

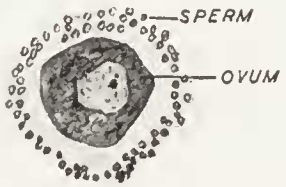

FIG. 20-RESULT OF CROSS 2

In crosses 2 and 3 very different results were seen. In 2 the sperm clustered in a ring about each ovum but at definite distance from it indicating that the ovum presumably secreted some bio-chemicals, which while attracting the sperm prevented them reaching the ovum and effecting fertilization (Fig. 20). The results of the third cross were negative.

Crosses 1 and 4 indicate that the sperm and ova used in the experiments were viable. The other two crosses (2 and 3) showed that the two species probably cannot interbreed and therefore are most probably separate biological species.

Paper partition chromatography.

In 1953 Buzzati-Traverso and Rechnitzer showed that comparisons of paper chromatograms obtained from tissue extracts of fishes indicated differences between species and the patterns so obtained were constant within a species irrespective of the size or age of the fish. The authors claim that comparable results were obtained in other phyla and suggest that the technique could be used to distinguish stocks of the same species belonging to geographically isolated populations. Buzzati-Traverso (1953) has also shown that paper chromatography of tissues of genetically known strains of *Drosophila melanogaster* and of certain plants gives a constant and distinctive pattern for each strain.

Following this work Kirk, Main and Beyer (1954) applied paper partition chromatography to seven species of land snails, two introduced species and five species native to Western Australia. The results of this work were in agreement with that of Buzzati–Traverso, the chromatograms obtained for each species being readily distinguishable from those of other species. They also compared chromatograms of one species from four widely separated localities and found no significant differences. Similarly differences in diet did not affect the resulting chromatograms for a particular species.

These results suggested that the method might be applicable to the present problem. Consequently several experiments were carried out with either adductor muscle or foot muscle from *K. rhytiphora* and *K. scalarina*.

Three techniques were tried including a modified version of the ascending chromatography described by Black, Lestrange and Zweig (1952). The most successful method was taken from Ceriotti (1956) which enabled a greater amount of tissue to be used and the chromatographing to be done at a slower rate thus allowing greater separation of the amino acids.

In this method a circle of Watermans No. 3 filter paper 24 cm. in diameter was held between two glass plates 25 cm. square, the lower one having a hole, 7 mm. in diameter, drilled in it. The material to be chromatographed was placed at the centre of the filter paper, above the hole in the lower glass plate and covered by a small circle of paper to prevent it coming in contact with the upper plate. A small circle of Watermans No. 3 filter paper was made into a cone and placed in a petri dish of solvent. The apex of the cone rested in the hole of the lower glass plate just touching the centre of the filter paper below the tissue. In all experiments the solvent was butanol : acetic acid : water (100:22:50 u/o) and they were carried out in a constant temperature of 22°C. The tissue used was dried for six hours in an oven at 100°C. and then ground to a fine powder. In both species the foot was used. For *K. rhytihpora* 11·8 mgr. were used and runs were for 3 hours 56 minutes; for *K. scalarina* 10·8 mgr. were used and the runs 3 hours 50 minutes long.

Ten chromatograms obtained were examined under ultra-violet light using a Hanovia 125 watt mercury vapour discharge lamp. The fluorescent and absorption bands were measured, 8 to 10 readings being taken on various radii of each chromatogram. The Rf values for each set of readings were calculated and the means for each species obtained. The means were as follows:—

	First fluorescent band. (cm.)	Second fluorescent band. (cm.)	Third fluorescent band. (cm.)
K. rhytiphora	0·58–0·53 Mean 0·55	0·40	0·30
K. scalarina	0·55	0·40	0·27

A comparison of the mean Rf value for each species shows that the differences are negligible, being the same for two fluorescent bands and only 00·3 different in the third. Also the fluorescent and absorption patterns and colours were the same for each species.

When considering the results of these experiments it must be remembered that the number of proteins in the animal body is great and that the solvent only removes a certain number which may or may not be those dependent on specific differences. Apart from the work of Buzzati–Traverso and Rechnitzer (1953), on fish, most of the later work has been done on *Drosophila melanogaster* and its mutant strains (Hadorn and Mitchell, 1951) and more particularly on lethal strains where abnormalities in the chemical equilibrium of the animal are present and there are, therefore, easily detectable differences. Thus the results of the above experiments do not indicate that there are no differences in the protein constitution of the two species only that the methods used have not revealed them. However until a suitable solvent is found this type of analysis is inapplicable to the present problem.

Commensal and parasitic animals associated with *K. scalarina* *K. rhytiphora*.

Only four commensal or parasitic animals were found in the course of this investigation and as yet the identification of each is arbitary or unknown.

The commensal sea anemone associated with *K. scalarina* was mentioned earlier, in the discussion of that species.

Both species were found to contain small crabs of the genus *Pinnotheres* (Family Pinnotheridae). There does not appear to be much literature on the Australian forms of this genus but from "The Crustaceans of South Australia" (Hale, 1927) the forms found seem to correspond with *Pinnotheres globosa* (Baker). However this species, according to Hale, is found in from five to ten fathoms of water in the molluscs *Chlamys bifrons, Spondylus tenellus* and *Modiolaria australis*. The specimens ranged from small immature females (2 mm. long) to larger mature animals 6 mm. long. Apart from occasional malformation of the ctenidia the crabs seem to have little affect on the *Katelysia*.

Encysted forms of an unknown parasite were observed in the blood vessels of the inner ctenidia of *K. rhytiphora*. These were seen only in sections. Likewise a small worm-like animal was found in a calcareous cyst in the body wall of a *K. scalarina*. This was thought to be of the phylum Acanthocephela.

Discussion.

The first part of this paper was written to sort out the complex synonymy of the three Australian species belonging to the genus *Katelysia*. Since writing, however, the writer has had access to two Japanese publications "Coloured Illustrations of the Shells of Japan" by Tetsuaki Kira (1959) and "An Illustrated Handbook of Shells in Natural Colours from the Japanese Islands and adjacent Territory" by Shintaro Hirase, revised and enlarged by Isao Taki (1954). These authors list among the lamellibranchs of Japan the species *Katelysia*

japonica Gmelin. As yet specimens of this species have not been examined and it is uncertain whether this species belongs in *Katelysia* sensu stricto or, as indicated by Kira, in *Hemitapes* Römer. Problems associated with this latter genus were mentioned earlier.

The particular investigation of the two species, *K. scalarina* and *K. rhytiphora* has shown that the shell features are sufficient criteria for separation of the two species, the experimental crossings having revealed that they probably cannot interbreed. Cotton and Godfrey (1938) comment that there is a gradation from *K. scalarina* to *K. rhytiphora* (*K. corrugata* in Cotton and Godfrey) but in all the specimens examined no such gradation of shell feature has been found.

However there is a wide variation in colouration both inside and outside; in the coarseness of ornamentation and in the convexity of the valves. This variation is dependent partly on local environmental conditions as for example estuarine conditions at Lakes Entrance, Victoria or those at Port Arthur, Tasmania. As yet the tolerance of the three species to changes in temperature and salinity is not known. Distribution suggests that they may be slightly tolerant to changes in salinity.

The anatomical studies did not reveal any marked differences in the gross anatomy of the animals though there were minor differences. The colouration of the siphons is different; the distribution and number of minor arteries, particularly to the visceral mass differs; the general shape of the visceral mass and foot is distinctive (corresponding to the shape and the dimensions of the shell) and the number of filaments to a plica of the inner ctenidia is different.

The results of the paper partition chromatography and the breeding survey have already been discussed. The breeding survey also showed that at no time were the populations devoid of mature and spawning individuals. This seems to indicate that breeding continues throughout the year with two periods of maximum activity in September–October and March.

This is different from the known breeding cycles of the Northern Hemisphere and suggests that at least in southern Australia there is a different breeding rhythm. Possibly there are no extremes in temperature sufficient to cause the cessation of breeding. Verification of this could possibly be made by determining the annual temperature range in Victorian and Tasmanian waters and investigating the breeding cycles of the same species in Tasmania.

The histological work revealed two points of general interest. The first is the mode of formation of the gastric shield. Two theories have been advanced, one by Yonge, the other by Gutheil. Although until the exact nature of the shield is determined biochemically, the mode of formation cannot be exactly given it seems from this work that Yonge's theory is highly improbable.

The other point is in connection with Yonge's suggestion that the mantle lobe is divided into muscular and sensory portions. This does not appear to be generally so and certainly in *Katelysia* there is no apparent concentration of muscular tissue in any particular portion and the nerves present are not restricted to any one part.

In conclusion the writer would like to thank all who have helped in this work. In particular, thanks are due to Dr. F. H. Drummond under whose direction this work was carried out, Mr. A. G. Willis for help with the histology, Dr. A. M. Clarke for help with the paper partition chromatography, Miss J. H. Macpherson for making available the shell collections of the National Museum of Victoria, Dr. D. MacMichael for making available the type *Katelysia enigma* held in the Australian Museum, Sydney, Mr. B. C. Cotton for making available specimens from the collection of the South Australian Museum, Dr. E. Binder for photographs of types held in the Musee d'histoire Naturelle, Geneva, Mr. E. L. Wilkins for comments on specimens in the British Museum, figured by Reeve in his Conchologia Iconica and Miss I. Bennett of University of Sydney.

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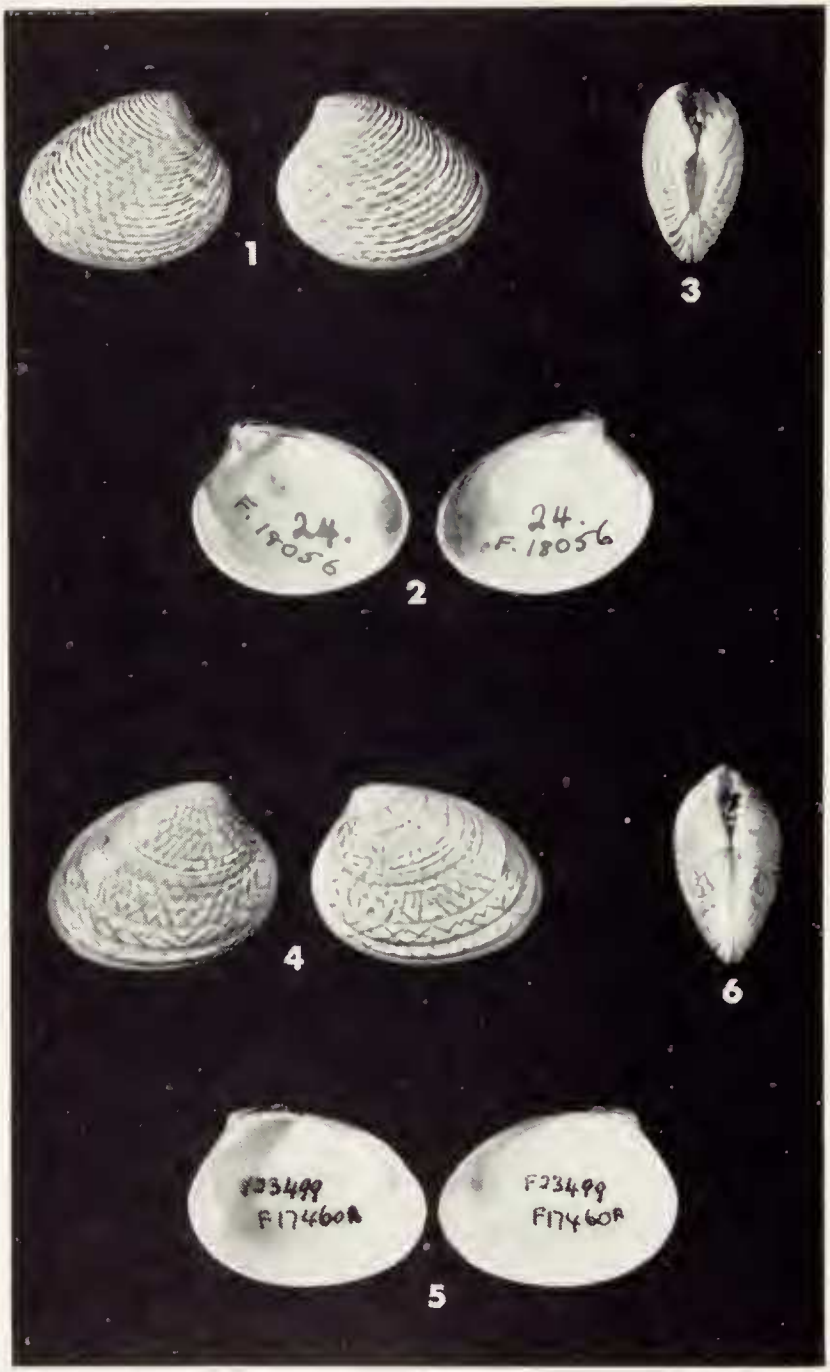

PLATE I.

Katelysia scalarina (Lamarck).

1. Exterior of valves; 2. Interior of valves; 3. Dorsal view showing umbos, ligamental area and lunule.

Katelysia scalarina variety *polita* sp. n.

4. Exterior of valves of holotype; 5. Interior of valves of holotype; 6. Dorsal view showing umbos, ligamental area and lunule.

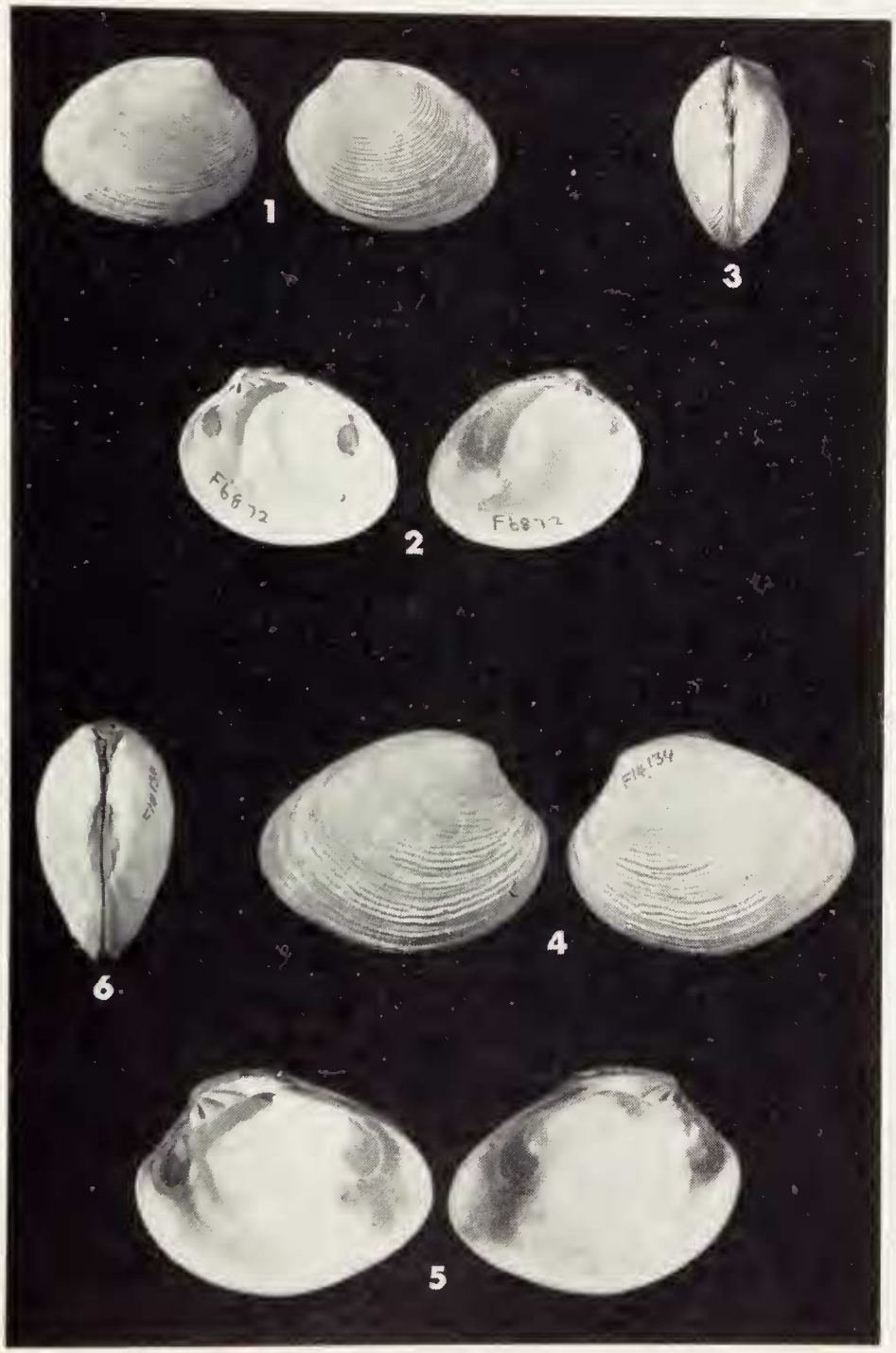

PLATE II.

Katelysia peroni (Lamarck).

1. Exterior of valves; 2. Interior of valves; 3. Dorsal view showing umbos, ligamental area and lunule.

Katelysia rhytiphora Lamy.

4. Exterior of valves; 5. Interior of valves; 6. Dorsal view showing umbos, ligamental area and lunule.